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POPULATION DYNAMICS OF THE FERRUGINOUS HAWK DURING A PREY DECLINE

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Abstract.— A nesting population of Ferruginous Hawks (*Buteo regalis*) at the eastern edge of the Great Basin in west-central Utah was studied for three nesting seasons, 1972-1974, during which time a significant decline in jackrabbit numbers occurred. The total number of hawks and nesting pairs varied throughout the study. In 1972, 16 pairs occupied territories and only 1 pair failed to nest. By 1974, however, only 5 pairs and 2 single birds occupied territories. The number of young fledged ranged from 31 in 1972 to 3 in 1974. The nesting phenology of the Ferruginous Hawk and the reproductive period of black-tailed jackrabbits are clearly correlated. Of the jackrabbit remains collected from hawk nests, 90 percent were from rabbits younger than 13 weeks. The decline in hawk numbers is thought to be directly correlated with a drop in the jackrabbit population.

How to get something to eat and how to keep from being eaten are among the most fundamental requirements of life. These factors have a tremendous impact on the structure, abundance, and community integration of an organism (Huffaker 1970: 327).

Much has been written about predation; yet many questions remain unanswered. Brown (1970: 247) suggested that seasons and breeding cycles of certain raptor species have never been properly correlated with behavior and abundance of their prey. In this study we sought to determine the effect of prey density on the nesting success of the Ferruginous Hawk (*Buteo regalis*) and to investigate the timing of predator and prey reproductive cycles and establish, if possible, a correlation between these two events. Finally, since little was known at the time of this study about the Ferruginous Hawk, we felt that any general knowledge of this species gained in the study would be of value.

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Methods and Procedures

The study was conducted from June 1972 through October 1974 within an area of approximately 932 km^2, involving portions of Utah and Tooele counties in northcentral Utah. Most of the field work was carried out during the nesting season, but we made monthly observations from October 1973 through October 1974. During the periods of intensive study, several visits were made to the study area each week (Fig. 1).

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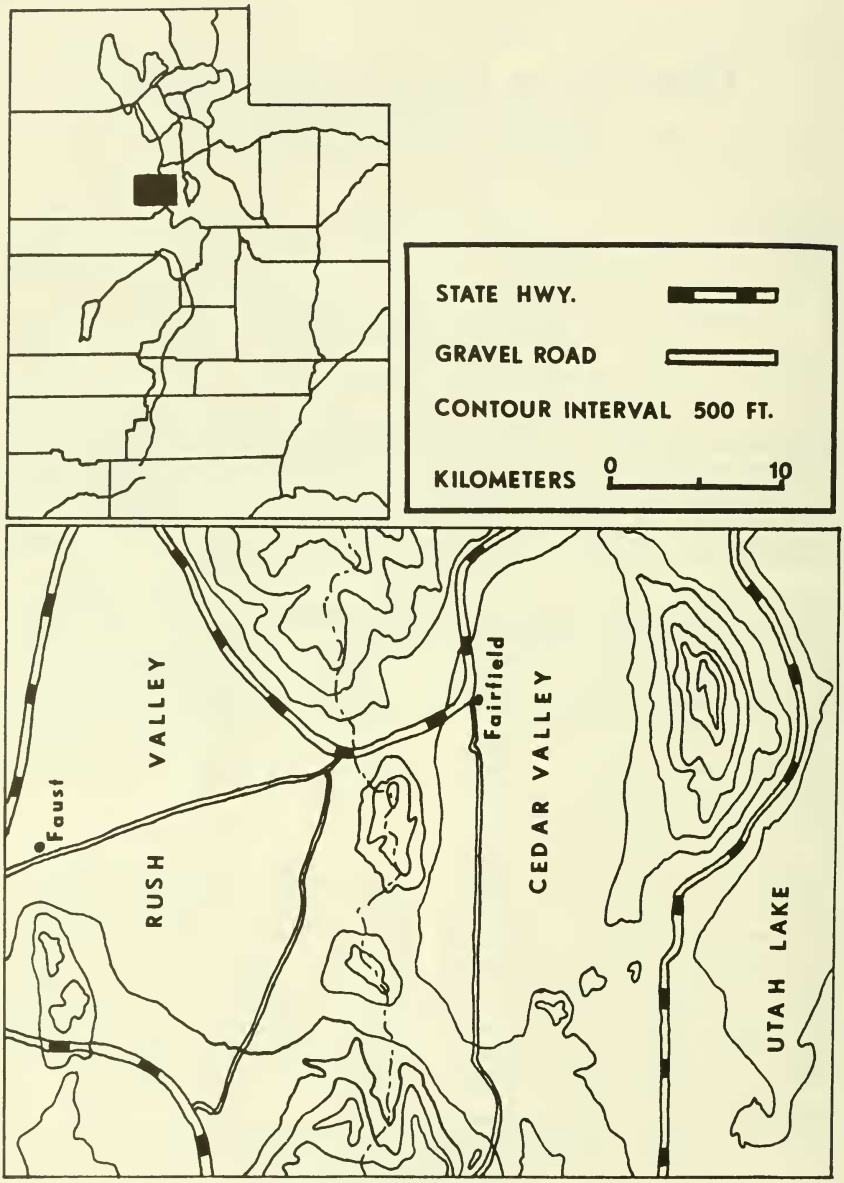

Fig. 1. Study area location.

A smaller portion of the overall study area (238 km²) was selected for intensive study. This area coincides approximately with the boundaries of Cedar Valley, one of the eastern valleys of the Great Basin valley-and-range complex.

The intensive study area, henceforth referred to as Cedar Valley, was systematically searched for Ferruginous Hawk nests in 1972 and 1973. Previous studies (Murphy et al. 1969, Smith and Murphy 1973) and banding records were also utilized in nest location and production for 1972 and previous years. An effort was made to locate inactive as well as active nests in both Cedar Valley and the western part of adjoining Rush Valley.

Prey remains and castings were collected regularly from the active nests. Identification of prey items was made by comparison to known specimens. The length of rabbit feet found in and around the nests was recorded and compared with tables in Haskell and Reynolds (1947) to estimate ages and weights.

Black-tailed jackrabbits (*Lepus californicus*) density indices were obtained by use of line transects. Five randomly distributed, square transects .25 km on a side (Gross 1967) were conducted periodically throughout the latter part of the study. The transect leg and direct distance from the observer to the point of flush was recorded for each rabbit flushed. The angle formed by the transect line and a line from the observer to the point where the animal was located was measured to the nearest degree.

Numbers of road-killed jackrabbits observed during regular visits to the study area as well as during winter raptor surveys were recorded. By expressing the number of kilometers traveled per road-killed jackrabbit, an index of abundance was obtained. During the latter part of the study, hind foot lengths were recorded for each road-killed jackrabbit.

Clutch size, fledging rates, and other production figures were determined by regular nest visits throughout the nesting season.

Statistical tests used include student "t" analysis of variance, and chi square tests. The level of significance is 0.05 unless stated differently.

Results

The black-tailed jackrabbit was abundant in the study area during the 1972 nesting season. It was not uncommon, during a visit to the study area, to see as many as 15 jackrabbits flush before the vehicle. Active nests during this season were cluttered with jackrabbit remains. One nest contained remains of at least 24 jackrabbits. Unfortunately, we were unable to obtain objective population densities. Gross et al. (1974), however, gave jackrabbit density indices for a nine-year period (1962-1970) for their northern Utah study area. The indices represented approximately the number of jackrabbits per km² (Gross et al. 1974: 27). They recorded in the autumn of 1970 a peak density of 71.4 jackrabbits per km². Stoddart (pers. comm. and in Howard 1975) reported a spring 1972 density of 47.1 jackrabbits per km² in the same area. This value dropped sharply to 9.7 km² in the spring of 1973. We assume that population densities in Cedar Valley were similar to those in northern Utah during the 1972 nesting season.

We also observed a decline in jackrabbit numbers between the 1972 and 1973 nesting seasons. One nest active in 1973 contained no rabbit remains. This nest was in the area of peak 1972 nesting density. An area of 27,225 m² near this nest was systematically searched four times for jackrabbits. One rabbit was flushed in each of the first three searches but none on the last search. The three flushes may have represented one individual.

In 1974 five randomly selected transects located throughout the study area were walked to establish jackrabbit densities (Table 1). These transects were similar to those used by Gross et al. (1974). Only one area had a density greater than one (1.0) rabbit/km² (Table 1). The number of kilometers per rabbit sighted varied from 0.46 in the area of highest densities to 8.0 in an area where only one jackrabbit was sighted.

In addition to the transects, during the first eight months of 1974 the number of road-killed jackrabbits observed was recorded. Over 19,948 km were traveled during this period and 122 jackrabbits were counted (Table 2), for an average number of 89.7 kilometers traveled per jackrabbit.

In spite of a lack of quantification, we feel that jackrabbit numbers dropped significantly in our study area, as they did in northern Utah, between the 1972 and 1973 nesting seasons. Numbers continued to remain low in 1974. This decline in prey numbers had a significant impact on the Ferruginous Hawk population in Cedar Valley.

The total number of birds and number of nesting pairs varied throughout the study. Table 3 summarizes these data for an eight-year period. In 1972, 16 pairs occupied territories in the intensive study area. There were no single birds present. Only one pair failed to make a nesting attempt. A total of nine pairs occupied nesting territories in 1973; of these, two pairs failed to nest. No single birds were observed. In 1974 five pairs of birds occupied territories; two pairs failed to nest and two single birds were observed occupying territories (Fig. 2).

TABLE 1. Number of transects, total rabbits observed, and mean density index of jackrabbits for Cedar Valley, 1974.

Location	No. Transects Walked	No. Rabbits Counted	Km/ Rabbit	Density Index Rabbits/ Km^2
Cat Hill	6	7	1.37	0.17
Long Point	10	35	0.46	1.33
Roadtop Hill	5	1	8.0	0.06
Carrol	11	16	1.1	0.32
Quarry	3	0	–	–

TABLE 2. Number of road-killed jackrabbits, January-August 1974.

Month	No. Roadkills	No. Km Traveled	No. Km per Roadkill
Jan	4	1310.5	327.6
Feb	0	1145.2	–
Mar	5	1163.7	232.7
Apr	4	569.1	142.3
May	8	1664.4	208.1
Jun	33	2002.5	60.7
Jul	46	2355.4	51.2
Aug	22	822.7	37.4
Totals	122	11033.5	90.4

The total population varied from 32 birds present in 1972 to 18 in 1973 and 12 in 1974. Single individuals were observed only in 1974. A marked decline occurred over the three-year study, with the peak population occurring in 1973 (32 birds) and a low in 1974 (12 birds). The average number of birds present (for the study period) was 20.7, with a range of 12-32. The average number of Ferruginous Hawks occupying territories from 1967 to 1970 was 19 (range 18-27). The average number for the study period did not vary significantly from the average for the four-year period 1967-1970.

In 1972 there were 14.85 km^2 per pair of birds in the intensive study area. This value increased to 26.24 km^2 and 34.03 km^2 for 1973 and 1974, respectively. It should be noted, however, that much of the habitat of Cedar Valley is unsuitable for nesting. The previous values are thus misleading because nests were placed on the hills surrounding the valley and no nests were found on the valley floor proper. The relative changes in nesting density during the study, however, would remain the same.

In 1972, 94 percent of the resident pairs nested. This value then dropped to 77.8 percent and 42.9 percent for 1973 and 1974. The average for the three year period was 71.6 percent.

CLUTCH SIZE.— Disturbance of Ferruginous Hawks during incubation is a significant cause of nest desertion (Powers et al. 1973, Olendorff 1973), and therefore few nests were visited during incubation. Thus, an accurate clutch size was not recorded for all nests. However, by extrapolating back from the number of young hatched, or in some cases fledged, a minimum clutch size

was obtained. Minimum clutch sizes will be given, but it should be kept in mind that the numbers presented probably underestimate the true clutch size.

Minimum clutch size varied from a high of 2.7 in 1972 to 2.1 and 2.4 in 1973 and 1974. The average clutch size for these three years is 2.4. More complete data on clutch size was obtained by Weston (Murphy et al. 1969) and Smith and Murphy (1973).

Mortality.— Nestling mortality was high during the study. Data are not available for the 1972 nesting season, but, based on the number of young fledged from each nest, mortality appeared to be negligible. An average nestling mortality of 49.5 percent was, however, calculated for the 1973 and 1974 nesting seasons. This value is significantly greater than the 13.3 percent average calculated from the 1967-1970 data (Murphy et al. 1969, Smith and Murphy 1973).

In 1973 when the nests were visited regularly during incubation, two of the three nests in the southeastern end of the study area failed. Four chicks were lost in these two nests. One of the two chicks in the third nest disappeared during the first weeks after hatching. This may have been a case of cannibalism, or the bird may have died and was then eaten. The agent responsible for the deaths of the other young birds is not known. The striped skunk *(Mephitis mephitis)* was observed in the area as was the coyote *(Canis latrans)*. A cliff near the nests was apparently used by Great Horned Owls as a roost. They or other raptors in the area could have taken the young. One nest was blown out of a tree during the 1973 nesting season. Thus, three of the six nests (50 percent) were completely destroyed, contributing to a nestling mortality of 42 percent.

High nestling mortality occurred during the 1974 nesting season. Three nests hatched a total of seven young and fledged only three. Each nest fledged one young hawk. One young bird large enough to leave the nest, approximately five weeks old, was found dead beside the nest. Examination suggested that it died of starvation. Earlier, approximately three weeks after hatching, one nestling had disappeared from

Table 3. Ferruginous Hawk territory occupation and nesting attempts, 1967-1974.

Year	No. Pairs	No. Single Birds	No. Territories Occupied	No. Nesting Attempts	Percent Nesting per Occupied Territories	Area per Territory Km^2	Location[5]
1967[1]	13	–	13	13	100	18.34	CV
1968[1]	14	–	14	14	100	17.02	CV
1969[2]	13	1	14	12	85.7	17.02	CV
1970[2]	9	2	11	7	63.6	21.65	CV
1971[1]	5	0	5	5	100	–	CV
1972	16	0	16	15	94	14.85	CV
1973	9	0	9	7	77.8	26.24	CV
1974	5	2	7	3	42.9	34.03	CV
1972[4]	8	0	8	8	100	–	RV
1973[4]	3	0	3	3	100	–	RV
1974	1	1	2	1	50	–	RV
1974	5	0	5	5	100	–	DV

[1]Data from Weston (1969)
[2]Data from Smith and Murphy (1973)
[3]Data from J. R. Murphy (pers. comm.) Less time was spent in the field during the 1971 nesting season than the other years here listed.
[4]Data from R. Ferris (unpubl. field notes)
[5]Abbreviations: CV = Cedar Valley, RV = Rush Valley, DV = Dugway Valley

the same nest, perhaps a victim of cannibalism. Two of three young were lost in another nest, the second 11 days after the first. The nestling mortality in 1974 was 57 percent.

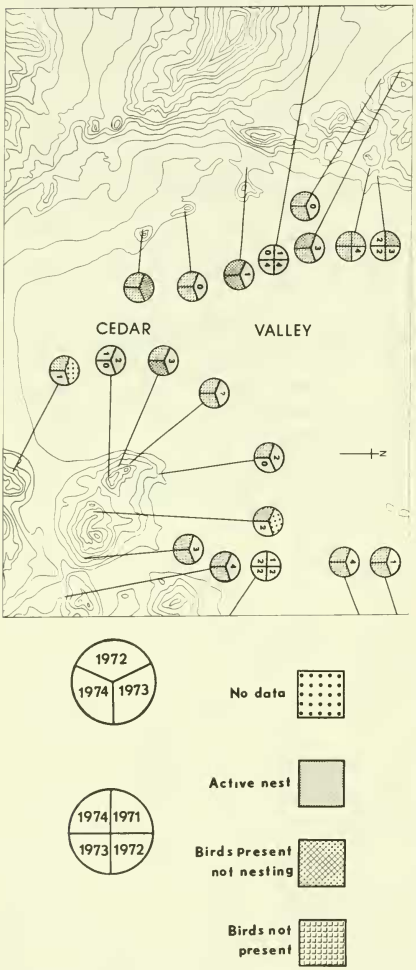

Fig. 2. Ferruginous Hawk nesting territories and young fledged, 1971-1974. Numbers within the sections of each circle represent the number of young fledged for that year.

Nest desertion.— None of the nests visited during the study were deserted by the nesting pair. However, visits were not made prior to laying or during incubation periods in two of the three nesting seasons. In 1973 regular visits were made to three nests during incubation. Although these nests were not deserted, our presence probably contributed to their failure (see previous section).

Renesting.— There were no renesting attempts during the study. In all cases when nests failed the pair continued to occupy the nesting territory. A visit to the territory after nest loss would still elicit normal nest defense behavior, although the degree of intensity was often reduced.

Fledging Success.— The number of young fledging declined drastically from a high of 31 in 1972 to 7 in 1973 and only 3 in 1974. Figure 3 summarizes these and oth-

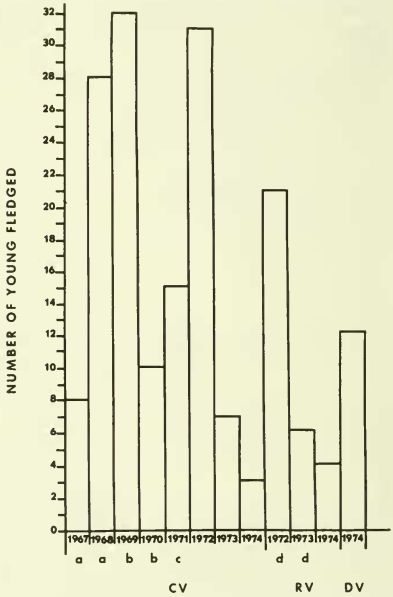

Fig. 3. Number of young fledged per year in Cedar, Rush, and Dugway valleys, 1967-1974.
[a]Data from Weston (1968)
[b]Data from Smith (1971)
[c]Data from J. R. Murphy (pers. comm.)
[d]Data from R. Ferris (unpubl. field notes)
Abbreviations are CV = Cedar Valley, RV = Rush Valley, and DV = Dugway Valley

er data for an eight-year period. The number of young fledging per nesting attempt ranged from 1.9 in 1972 to 0.7 in 1973, and 1.0 in 1974 (Figs. 2 and 4).

Figure 4 gives the number of nests fledging one, two, three, and four young, respectively. In 1969 and 1972 the number of nests fledging three or four young was much greater than the number fledging one or two. In 1973 and 1974 the reverse was true; in fact, the maximum number of young fledged from any nest in these two years was two.

Age of Jackrabbits Taken as Prey.— Measurements of jackrabbit hind feet taken from nests were compared with tables in Haskell and Reynolds (1947) to determine ages (Fig. 5). The age distribution was trimodal. Thirty-one (44 percent) of the 71 rabbits were from 2 to 6 weeks old, 32 (45 percent) of the total were from 8 to 12 weeks of age, and 7 (10 percent) were 16 weeks or older. Of the total rabbits found in Ferruginous Hawk nests, 90 percent were 12 weeks old or younger.

Figure 6 gives the age distribution of road-killed rabbits during June, July, and August of 1974. Fifty-seven percent of these rabbits were less than 13 weeks of age.

Nesting Phenology and Jackrabbit Reproduction.— Gross et al. (1974) found four reproductive peaks in the black-tailed jackrabbit, the first commencing approximately mid-January and others occurring at intervals of 40 days (Fig. 7). Figure 7 gives the approximate birth dates of these four litters and the average size of each. Superimposed on the graph are important dates in the nesting phenology of the Ferruginous Hawk. It appears that the hawk's nesting period is closely correlated with the reproductive period of the jackrabbit.

Discussion

Commencing with a peak in 1972, black-tailed jackrabbit populations declined throughout the study period. Gross et al. (1974) found that in their Curlew Valley study area, jackrabbit numbers reached a peak in 1970, then declined in 1971 and 1972. Numbers then dropped precipitously in the spring of 1973 (C. Stoddart pers. comm.).

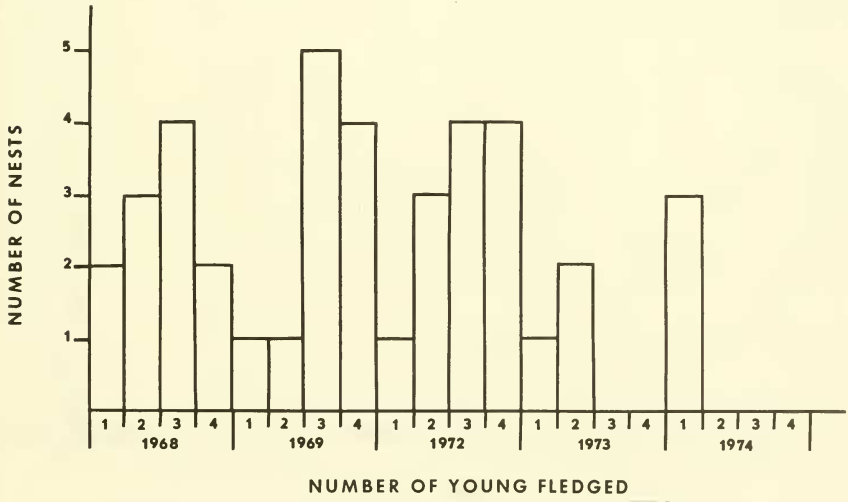

Fig. 4. Number of Cedar Valley Ferruginous Hawk nests fledging 1, 2, 3, and 4 young, 1968-1974.
[a]Data from Weston (Murphy et al. 1969)

We assume that jackrabbit numbers in our study area were similar to those in Curlew Valley, 192 km to the north, prior to 1973, inasmuch as jackrabbits were numerous in 1972 at least on the east side of Cedar Valley. The hawk nests located that year were cluttered with numerous rabbit remains, and hawk production was at its highest point of the study.

Smith (unpubl. ms.) reported a drop in jackrabbit numbers between 1969 and 1970. His observation corresponds closely with those made by Gross et al. (1974).

We observed a decline in rabbit numbers between the 1972 and 1973 nesting seasons. This decline coincided with a fivefold decrease in jackrabbit densities for the same period in Curlew Valley (C. Stoddart pers. comm.). An area of 27,225 m^2 in the eastern portion of Cedar Valley was systematically searched four times for jackrabbits during the 1973 nesting season. Only one rabbit was seen. An active nest near this area had no evidence of rabbit remains. During the 1974 nesting season, transects were made in various parts of the study area (Table 1). Only one area had a density greater than one rabbit per km^2. The number of kilometers per rabbit sighted varied from a high of 0.46 to a low of 8.0 in an area where only one rabbit was sighted during the study. Smith (unpubl. ms.) flushed 4.3 rabbits per km during 1970 (0.23 km/rabbit), the year of lowest jackrabbit densities during his four-year study. This value is twice as large as the comparable one for our study.

In the first eight months of 1974, the number of road-killed jackrabbits was recorded. Over 10,000 km were traveled during this period, and only 122 jackrabbits were seen. The average number of km traveled per jackrabbit was 89.7 (Table 2).

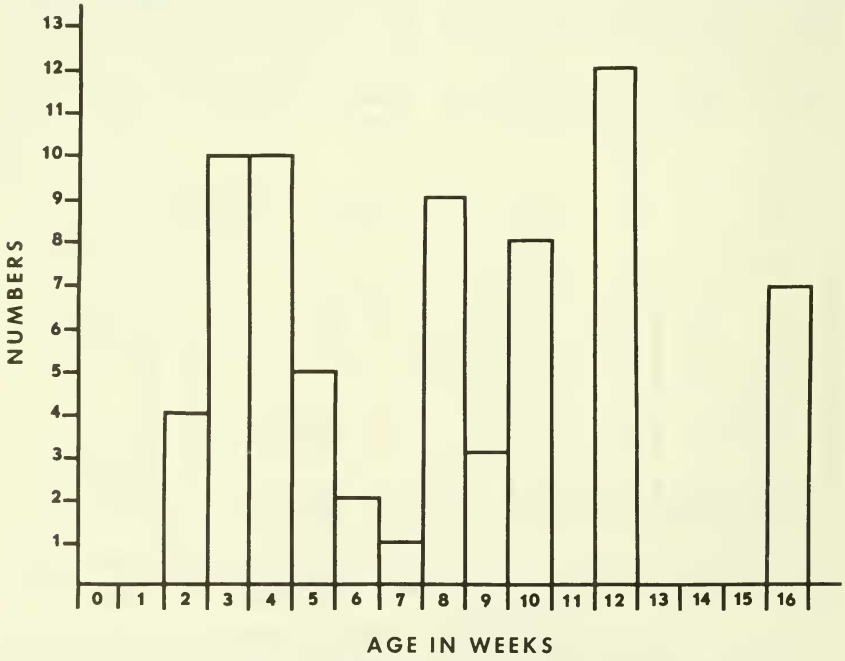

Fig. 5. Number and ages in weeks of jackrabbit prey remains from Ferruginous Hawk nests, 1972-1974.

Adams and Adams (1959) made similar surveys and found the frequency of road-kill per km far exceeded the value we obtained.

Breeding success of the Ferruginous Hawks was higher on the eastern side of Cedar Valley. The western side of the valley, although it does contain some small areas of good rabbit habitat, does not have as much prime habitat as the eastern side. In times of high densities this marginal habitat was utilized by jackrabbits, which in turn allowed hawks to utilize an otherwise unsuitable area.

We believe this helped produce the peak Ferruginous Hawk populations in the late 1960s and early 1970s. We believe that rabbits began to decline first in areas of marginal habitat, where they were most vulnerable to predation, and finally in areas of suitable habitat. Hence, a decrease in rabbit numbers occurred first in the western part of Cedar Valley and then in the eastern sections, producing a similar pattern in the Ferruginous Hawk populations.

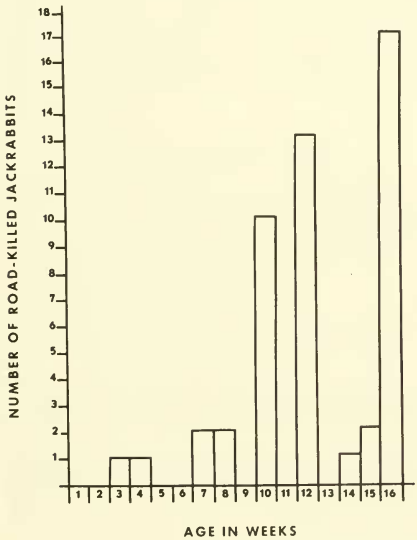

Fig. 6. Age distribution of road-killed jackrabbits, 1974.

Dependence on Jackrabbits.— Weston (Murphy et al. 1969) found that jackrabbits made up a major portion of the Ferruginous Hawk diet. Kangaroo rats were found more frequently as prey remains, but their biomass was not as great as that of the jackrabbits. Howard (1975) found that jackrabbits made up 86 percent of the biomass of the three main prey species. Smith and Murphy (1973) indicated that jackrabbits made up from 93 percent to 95 percent of the prey biomass in their study. In Rush and Cedar Valleys, jackrabbits are used extensively as a food source when young hawks are in the nest. One active nest in Rush Valley in 1972 contained the remains of at least 24 rabbits. In 1973 no active nests were found in Rush Valley.

Alternate Prey Species.— Ground squirrels were scarce in both valleys. Only three white-tailed antelope ground squirrels *(Ammospermophilus leucurus)* were seen in the two valleys over the entire study period. Townsend ground squirrels *(Citellus townsendii)* were more common, but scarce. Jackrabbits made up the only plentiful mammalian prey. When a decline in rabbit numbers occurred, alternate prey was thus not available in sufficient numbers for the hawks to maintain their numbers, and the evidence indicates that the decline we have outlined is due to the drop in jackrabbit numbers.

Townsend ground squirrels were more numerous in Dugway Valley, which is approximately 85 km west of Cedar Valley. Prey populations in this valley were not quantitatively sampled but ground squirrels were evident in large numbers during each visit to the area, and Ferruginous Hawks were correspondingly more successful as nesters. There, only three (20 percent) of 15 nestling hawks failed to fledge. One nest failure accounted for two of these three deaths. The nesting success of the Dugway Valley hawks was evidently due to the presence of a broad prey base. Therefore, our results, perhaps, apply only to areas where jackrabbits are the staple food of this hawk.

Population Dynamics.— From 1968 to 1974, the numbers of pairs of Ferruginous

Hawks in the study area declined steadily (Table 3). In 1972, 16 pairs were present and only one pair failed to nest. In 1973, 9 pairs occupied territories in the intensive study area, and 2 pairs failed to nest. Finally, in 1974 the number of hawks in the study area dropped to 12 individuals—5 pairs and 2 single birds. Two of the 5 pairs failed to nest.

R. Ferris (pers. comm.) documented a similar decline in Ferruginous Hawk numbers in Rush Valley (Table 3). Swartz et al. (1973) observed an increase in the number of nesting pairs of Rough-legged Hawks *(Buteo lagopus)* in Alaska, from 35 pairs in 1968 to 82 pairs in 1970; then the number of nesting pairs plummeted to 10, and only 2 young were fledged in 1972. Tubbs (1974) documented a similar decline in the Common Buzzard *(Buteo buteo)* in Great Britain. In these studies, as in ours, prey numbers declined drastically prior to the decline of raptor populations. The data imply a direct correlation between predator and prey fluctuations.

Habitat Vacancy.— In general, birds of prey occupy the same nesting territory for more than one year (Craighead and Craighead 1969). Nesting territories can thus be conveniently checked each year in the early spring and throughout the year for the presence of nesting birds. In 1972, 16 nesting territories were occupied. Only 9 territories were occupied in 1973, and 7 in 1974. The number of territories that were occupied declined each year, and previously active nesting territories were vacant (Table 3). Keith (1966) outlined the extent of vacant habitat of snowshoe hares *(Lepus americanus)* during a decline. A similar phenomenon of previously occupied habitat being vacant occurred with the Ferruginous Hawk in our study area (Fig. 2).

Davis et al. (1969) found that woodchucks

Fig. 7. Number and mean litter sizes of jackrabbits in Curlew Valley, with important dates in Ferruginous Hawk nesting cycle. Vertical lines represent jackrabbit litters. The horizontal line gives important events in Ferruginous Hawk nesting cycle. 1 = territory selection, 2 = mean laying date, 3 = mean hatching date, 4 = mean fledging date, and 5 = mean migration date.

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(Marmota monax) that were removed from one section of their study area were promptly replaced by immature woodchucks apparently from neighboring areas. Carrick's (1963) work with Australian Magpies *(Gymnorhina tibicen)* suggested that a group of unmated birds was present in his study area, and any vacancies in the breeding group were filled by members of this unmated group. Vacant territories were not filled by extra individuals nor was a group of nonbreeding birds observed in the present study with the Ferruginous Hawk.

Although 31 young were fledged in 1972, no young hawks were seen in the study area in 1973. Whether young hawks return to the place of their birth their first year is not known. Mortality rates for this period are also unknown. Craighead and Craighead (1969) suggested that as many as 88 percent of young hawks may die their first year. Hickey (1952) found annual mortality to be approximately 59 percent in yearling Marsh Hawks *(Circus cyaneus)* and 30 percent for the adults. Based on production of the previous year, even if mortality rates were as high as those listed here, a stable population size could be expected. We suggest that prey densities rather than mortality are responsible for the 1973 and 1974 population declines.

In 1972 all of the birds present on the east side of Cedar Valley nested and successfully fledged young, while at least three pairs on the west side did not. One pair on the west side of the valley did not nest. Two pairs that laid one and two eggs, respectively, did not hatch young.

In 1973, three pairs were present on the west side of the valley. One pair fledged two young, one pair failed to nest, and the other pair's nest was blown from the tree. On the east side of the valley four pairs were present, plus a single bird. Though all four pairs built nests and laid eggs, over 50 percent of the eggs failed to hatch and only four young were fledged from these four nests.

In 1974 four nest sites were occupied on the west side of the valley. One pair laid one egg, but none of the other birds laid eggs, although some nest building occurred. In the same year on the east side of the valley two pairs and one single bird occupied territories. Each of the pairs successfully fledged one of the three young that hatched in each nest.

Clutch Size.— The average clutch size was 2.7 in 1972, 2.1 in 1973, and 2.4 in 1974. The overall average of 2.4 is lower than the 3.3 average reported by Weston (Murphy et al. 1969) and Smith and Murphy (1973). Platt (1971) reported an average clutch size of 3.5 for 11 pairs of Ferruginous Hawks in Curlew Valley, and Howard (1975) reported an average clutch size of 2.78 and 2.77 for 1972 and 1973 in the same area. His method of gathering clutch size data was similar to that of our study.

Smith and Murphy (1973) found that clutch sizes vary from two to four eggs. Olendorff (1973) and Howard (1975) reported clutch sizes from one to five eggs. Clutch sizes of from one to four eggs were observed during this study. Clutches containing one and two eggs occurred frequently in areas of low prey numbers. Howard (1975) found 11.6 percent of the clutches examined contained only one egg, but correlation was not made between these nests and prey densities; the data imply that one- and two-egg clutches were correlated with low prey densities.

Fledging Rate.— The number of young fledged per year declined over the study period (Fig. 3). Thirty-one young successfully fledged in 1972, an average of 1.9 per active pair. This value dropped to one young per active pair in 1974; however, there were only three active pairs (Table 1). The overall average fledging rate was 1.2. The number of nests fledging two or more young decreased over the study period (Fig. 4). The reduction of young fledged per nesting pair was evidently correlated with a reduction in prey numbers.

Nestling Mortality.— The low prey abundance was an important factor in nestling mortality. The female from one nest was observed 5.2 km away actively hunting at a time when normally she should have been at the nest brooding the young. Nests

were visited periodically after hatching occurred. On a few occasions two nests containing small young were visited, but no adult birds were observed. Howard (1975) also examined nestlings without observing the adult birds in the area. On one occasion we observed a Swainson's Hawk *(Buteo swainsoni)* coursing low over an active Ferruginous nest, but no adult Ferruginous Hawks were observed. The absence of adults from the nest at this time was unusual, as almost always when a nest was approached at least one bird and usually two would begin to display and defend the nest as soon as the investigator left his vehicle.

This apparent nest inattentiveness would enhance the chance of chick mortality both from predation and exposure. We suggest that the high nestling mortality rate in 1973 (43 percent) was due in part to this behavior. The behavior resulted, we feel, from the additional pressure placed on the female hawk to provide herself and young with food, since the male was unable to provide adequate amounts.

C. White (pers. comm.) found that Rough-legged Hawks on the Alaskan tundra were not attentive at the nest when prey density was low. On one occasion he saw a Golden Eagle eating young Rough-legged Hawks at the nest while the adults soared over the tundra some distance away.

The nestling mortality in 1974 was 57 percent. During this nesting season, three nests hatched a total of seven young and fledged only three.

Responses to Lower Prey Densities.— Pairs in areas of low prey densities either failed to nest or laid smaller clutches. Single birds, although they occupied nesting territories, did not mate during the nesting period. In those pairs that laid larger numbers of eggs, the female as well as the male was forced to spend periods away from the nest to supply food for the young. As a result, in many cases, the number of eggs hatched and young fledged was low.

Otteni et al. (1972) found that Barn Owls *(Tyto alba)* raised 1.5 times as many young per pair in years when prey was abundant as in years when prey populations were more limited. McInvaille and Keith (1974) reported a numerical increase in a Great Horned Owl *(Bubo virginianus)* population in response to a cyclic increase of snowshoe hares. Shelford (1943) observed that the population of Snowy Owls *(Nyctea scandiaca)* in the Arctic is directly dependent upon the abundance of lemmings (*Lemmus* spp. and *Dicrostonyx* spp.). During years when lemming populations were low, the owls failed to nest or laid only one or two eggs. In years of high prey populations the percentage of owls nesting was high, and each pair raised many young (maximum of 12). Pitelka et al. (1955) recorded similar correlations for Snowy Owls and Jaegers *(Stercorarius spp.)*. Southern (1970) found that the percentage of Tawny Owls *(Strix aluco)* that nested during low prey years was near zero; however, in years of abundant prey, nearly 100 percent of the owls nested.

Murphy (1975) found that the Golden Eagle population in central Utah experienced a decline in numbers of nesting pairs during the period of this study. He suggested that there was strong evidence to indicate that this trend was also related to population fluctuations of the black-tailed jackrabbit.

Howard (1975) also reported a decline in Ferruginous Hawk numbers and attributed it to a drop in jackrabbit numbers. We suggest that the Ferruginous Hawk responds to fluctuations in prey densities in a similar fashion to the other species discussed above.

Nest Abandonment and Renesting.— Olendorff (1973) and Powers et al. (1973) suggested that Ferruginous Hawks are quick to abandon their nests if disturbed during nest building or incubation. In 1967, Weston (Murphy et al. 1969) reported that three nests containing eggs and four nests ready for eggs were abandoned early in the nesting season after only one visit to each nest. The next year, although identical nest observation procedures were conducted, no nests were abandoned.

We visited three active nests regularly during the 1973 nesting season. None of these three nests was abandoned, nor did

we observe any nest abandonment during the entire study. However, the young of two of these nests were destroyed by something. We feel that our presence at the nest was probably responsible to a large degree for these deaths, because some carnivores are known to follow human tracks. Willis (1973) reported the destruction of Ant Bird *(Gymnopithys bicolor)* nests by predators after a routine visit. Ray (1968) suggested the use of napthalene crystals around the nest and on paths to destroy the scent trails made by the investigator. Olendorff (1973) outlined methods of handling and times and duration of visits that will have the least injurious effect on the research subjects. An investigator would be wise to contemplate the impact of the study on the population prior to commencing his or her work. The methods outlined in the references above may be valuable research tools that could decrease the amount of investigator-caused losses to young birds.

Many raptors will lay a new clutch of eggs if all eggs are taken shortly after completion of the clutch (Olendorff 1971). No renesting occurred during this study even though several nests were destroyed, including one nest that was blown out of a tree shortly after the time when the clutch should have been completed. The pair from one of the aforementioned nests that had successfully hatched three young, only to have them destroyed, moved 0.4 km east and defended an alternate nest site. Less than a dozen sticks were piled on top of a rock at this new location. Despite this, the pair actively defended this token nest.

Age of Rabbits Taken as Prey.— The hind legs of 71 jackrabbits were collected from active nests throughout the study. The length of the hind foot was compared with tables in Haskell and Reynolds (1974) to determine age. A trimodal distribution was noted (Fig. 5). Thirty-one (44 percent) of the 71 rabbits were from two to six weeks old, 32 (45 percent) of the total were between eight and twelve weeks of age, and 7 (10 percent) were sixteen weeks or older. Of the total rabbits found in Ferruginous Hawk nests, 90 percent were less than thirteen weeks of age. Similar results were reported by Dunnet (1957) in Australia where avian predators were selectively killing young rabbits. He found that when the rabbits reached three months of age they were no longer vulnerable to the intense avian predation to which they had been subjected earlier.

The adult Ferruginous Hawks were clearly utilizing the immature jackrabbits to a much greater degree than the older rabbits. This is not surprising, because during the nesting season there are more immature than mature rabbits available to the hawks, and the young rabbits would undoubtedly be easier to catch, kill, and carry.

Nesting Phenology and Jackrabbit Reproduction.— Gross et al (1974) found four reproductive peaks in the black-tailed jackrabbit, the first commencing approximately mid-January and others occurring at intervals of 40 days (Fig. 7). The first two litters are born prior to the selection of territories by the Ferruginous Hawks. In some cases the hawks do not even return to the nesting area prior to the birth of these two litters. During years of good rabbit production, litters one and two should provide an abundant prey source for the courting hawks. After the nest has been constructed, egg laying begins (Fig. 7). During egg development an ample supply of prey may be as important as when young are in the nest. Average clutch sizes from years of good rabbit numbers are larger than those calculated for years of low rabbit numbers (Smith and Murphy 1973).

The average clutch size for 1972 was 2.7, but for 1973 and 1974 it was 2.1 and 2.4, respectively. In 1972 one nest on the west side of Cedar Valley contained a single egg, another only two eggs. In both cases hatching did not occur. Also, a pair in this same area failed to nest. There is a general lack of good rabbit habitat on the west side of the study area. Data for years other than 1972 indicate fewer rabbits in this area than the eastern side of the valley. Although the data do not unquestionably support the thesis that fewer eggs are laid when prey is scarce during periods prior to egg devel-

opment, it appears that such a trend did occur in this study as well as in the investigation conducted by Shelford (1943) on the relationship of Snowy Owl response to low prey densities.

We suggest that the timing of the arrival of the Ferruginous Hawk in its nesting territory is correlated with the presence of a suitable prey base in the form of coinciding litters of rabbits that are available for prey during prelaying activities. Rabbit litter three is born just prior to egg laying by the hawks. This is the largest of the three litters, averaging 5.2 young per pregnant female (Gross et al. 1974). During incubation in many raptor species the female hawk does most of the brooding and the male supplies her with food (Brown and Amadon 1968). If the male has little trouble supplying both himself and his mate with food during this period, the female apparently needs to leave the nest infrequently during the incubation period. A large number of young jackrabbits of approximately 1 to 12 weeks of age would be available to a Ferruginous Hawk pair that occupied a suitable territory throughout the period of incubation during a year of good rabbit densities. This presumptive age distribution compares favorably with the distribution of the ages of rabbits actually taken from the nest (Fig. 5). Members of the first litter would be approximately 12 weeks of age at the time of laying and would still be available to the hawks during incubation.

Shortly after hatching, rabbit litter four is born. Litter three would be approximately four weeks of age, and litter two approximately twelve weeks of age at this time. The three largest litters are thus available for food as the young hawks develop. The members of litter four are less than five weeks of age while the young hawks are in the nest. Based on ages of rabbits taken to the nest, three of the four litters (litters 2, 3, and 4) are available for use as food for the nestling hawks. The last two litters probably provide the majority of the rabbits utilized as prey during hawk development.

After the young hawks leave the nest they remain in the area for approximately one month prior to migration. Rabbit litter four is approximately 10 weeks old at this time, and probably provides the major portion of the food supply of the young hawks. Young hawks likely cannot catch adult rabbits or even young of that year other than members of litter four. The timing of departure could well be correlated with a decline in available prey. Data from rabbit transects made during the nesting season in 1974 indicate that this may be so, inasmuch as jackrabbit densities declined throughout the nesting season.

Other raptors migrate at approximately the same time as the Ferruginous Hawk (August 1). A. Jenkins (pers. comm.) noted a peak in migrating hawks along the Wasatch Front in late August. Although some buteos were observed, most migrants were accipiters and falcons. Olendorff (1973) recorded the Ferruginous Hawk as a resident species in the Pawnee Grassland of Colorado. It is not known why this species should be migratory in central Utah, yet resident in a location only about 800 km to the east. In both locations an influx of wintering raptors occurs, primarily Rough-legged Hawks and Bald Eagles *(Haliaeetus leucocephalus).* In Utah the Ferruginous Hawks have migrated before these species appear. Competition does not seem, then, to be the factor of importance. We suggest that perhaps prey availability dictates time of migration. Further light could be shed on this hypothesis if more were known about the wintering areas and food habits of the Ferruginous Hawk.

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